29: 119-140

Published online 17 May 2018

# By their fruit you will recognise them: species notes and typifications in Western Australian species of *Opercularia* (Rubiaceae: Anthosperminae)

## Adrienne S. Markey

Western Australian Herbarium, Biodiversity and Conservation Science,
Department of Biodiversity, Conservation and Attractions,
Locked Bag 104, Bentley Delivery Centre, Western Australia 6983
Email: Adrienne.Markey@dbca.wa.gov.au

#### **Abstract**

Markey, A.S. By their fruit you will recognise them: species notes and typifications in Western Australian species of *Opercularia* (Rubiaceae: Anthosperminae). *Nuytsia* 29: 119–140 (2018). An examination of herbarium collections, type material and reference to original species descriptions has found that several species names of *Opercularia* Gaertn. have been misapplied in Western Australia. This nomenclatural confusion stems from a combination of missing types, a lack of reference to either types or correctly identified specimens, and no recent revisions of the genus. Previously presumed to be extinct, *O. acolytantha* Diels is neotypified and discussed here as an extant species endemic to the Mallee and Esperance bioregions of Western Australia. *Opercularia hirsuta* Benth. is found to be a far rarer species than previously thought, with no material matching the type collected since the 1860s. *Opercularia nubicola* A.S.Markey is described as a new species with affinities to *O. aspera* Gaertn. *Opercularia rubioides* Juss. is reduced to synonymy with *O. aspera*,which is excluded from Western Australia. *Opercularia scabrida* Schltdl. is also excluded from Western Australia. This paper provides updated notes, illustrations and a key to Western Australian species of *Opercularia*. Characteristics of the infructescence, fruits and seed are diagnostic for these species and are illustrated here for this purpose.

## Introduction

Opercularia Gaertn. (Rubiaceae: Anthosperminae) is a genus of 18 species of perennial low shrubs or herbs endemic to southern Australia. Eleven of these species are all endemic to the south-west of Western Australia (Western Australian Herbarium 1998–; Council of Heads of Australasian Herbaria [CHAH] 2006–). Plants have a characteristically foetid odour when the leaves are crushed; hence 'stinkweed' being one vernacular name for the genus. Opercularia is named for its unusual infructescence, which is either a simple capsular syncarpium (in some species) or more commonly a compound globular capsiconum (Spjut 1994) of several capsular syncarpia, each of which formed from several sessile fruits fused by their pericarps (Jussieu 1804; Bentham 1867). The syncarpium itself is a two-valved compound capsule, the inner valves fused together to form an apical operculum which abscises from the compound capsule to release the seeds. Two species (O. acolytantha Diels and O. liberiflora F.Muell.) lack the characteristic operculum and fruits fused into syncarpia, instead having sessile free (unfused) flowers and single fruits arranged on a common receptacle into a solitary, globular capitulum.

There have been few updates addressing Western Australian species of Opercularia since Mueller (1863–4), Bentham (1867) and Diels and Pritzel (1904–5), apart from three regional flora treatments (Blackall & Grieve 1982; Rye 1987; Wheeler 2002) and a new species described by Keighery (1999). This paucity of recent work has resulted in some nomenclatural confusion and errors in applying names to collections in Western Australia. This was found to be particularly evident among Opercularia specimens at the Western Australian Herbarium (PERTH) for O. acolytantha, O. hirsuta Benth. and O. rubioides Juss. Furthermore, while eastern states herbaria house several collections of O. scabrida Schltdl., none exist at PERTH. Misidentifications of collections have been compounded by a lack of reference to either the type material or older collections cited by Bentham (1867) and Mueller (1863-4), probably because these are held by interstate or overseas herbaria or, in the case of O. acolytantha, the type being missing. Three of these four species are of conservation concern; O. acolytantha has been declared extinct (Department of the Environment and Energy 2018), while O. hirsuta and O. rubioides are poorly known taxa with Priority Two and Priority Three state conservation listings, respectively (Smith & Jones 2018). This confusion in identifying species of Western Australian Opercularia is greatly hampering the assessment of conservation status, the monitoring of known populations and the survey for new populations of these rare and poorly known species. This research paper aims to assess the taxonomic and conservation status of these four problematic species. While a modern revision of the genus is desirable, for the interim this paper provides updated notes, typifications, morphological descriptions, illustrations and an updated key for Western Australian species.

### Methods

Specimens of *Opercularia* at the Western Australian Herbarium (PERTH) and National Herbarium of Victoria (MEL), and loans from the Australian National Herbarium (CANB) were examined using light stereomicroscopy, and further information was gained from scans of sheets held at Muséum National d'Histoire Naturelle, Paris (P), Kew (K), and the Natural History Museum of the United Kingdom (BM). Measurements are mostly based on dried specimens, with additional measurements and observations obtained from alcohol preserved and fresh material of *O. acolytantha*, *O. echinocephala* Benth., *O. hispidula* Endl., *O. vaginata* Juss. and *O. volubilis* Benth. Fieldwork was undertaken at several localities (Porongurup National Park, South Stirling Nature Reserve, Stirling Range National Park, Cape Le Grand National Park, and the Oldfield River estuary) to relocate populations of *O. acolytantha*, *O. hirsuta* and *O. rubioides*.

Terms used here to describe outgrowths of the indumentum are papillae (protuberances that are slightly emergent epidermal cells or a projection of the epidermal cell wall) and hairs (elongate, unbranched trichomes) (cf. Hewson 1988). It is acknowledged that the distinction between these two groups is not clear-cut, as papillae may grade into very short, stiff hairs with broad bases (this is particularly so for O. aspera Gaertn. and O. nubicola A.S.Markey). While these two broad terms are used here, a refinement of terms for the range of features that comprise the indumentum of Opercularia is warranted in any future revisions of the genus.

Differences in seed morphology among Western Australian species are illustrated in Figure 1. The term capsiconum, as defined by Spjut (1994) applies to the globular compound infructescence found in species where several capsular syncarpia have fused into a single spherical unit.

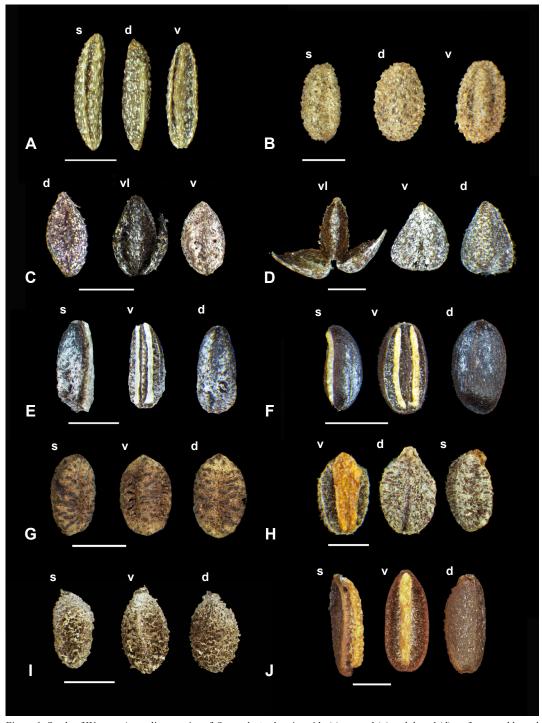


Figure 1. Seeds of Western Australian species of *Opercularia* showing side (s), ventral (v) and dorsal (d) surfaces, and lateral appendages separated from the ventral keel (vl) in two species. A – O. hirsuta (G. Maxwell s.n.); B – O. hispidula (P.G. Wilson 3974); C – O. acolytantha (W.R. Archer 1212936); D – O. vaginata (G. Keighery 13019); E – O. nubicola (A.S. Markey & S. Dillon SR 9656); F – O. echinocephala (A. Markey & S. Dillon NIB 9643); G – O. liberifolia (A.S. George 6878); H – O. volubilis (A.S. George s.n.); I – O. spermacocea (G.J. Keighery & N. Gibson 304); J – O. apicifolia (P.G. Wilson 3967). Scale bars = 1mm. Photographs by A. Markey.

## Key to Western Australian species of Opercularia

- Individual flowers and fruit free on common receptacle of a globular inflorescence; operculum absent, fruits separating from receptacle as an entire dispersal unit
- 1: Ovaries of several flowers coalesced into a unit and arranged either singly or with other capitula on a globular inflorescence; basic unit of fruit a capsular syncarpium with the inner valves forming an operculum (lid) which separates from outer valves by operculate dehiscence to release the seeds
  - 3. Peduncles terminal or axillary, terminal peduncles erect or nearly so, 10–60 mm long, slightly to considerably longer than subtending leaves; leaves linear, narrowly ovate or narrowly obovate, sessile or near-sessile; inflorescence a compound capitulum, infructescence a capsiconum

    - **4:** Plants scabrous to glabrous; leaves filiform, linear or narrowly ovate, apex acute to apiculate; seeds obovate or elliptic in outline, furrows and keel present but inconspicuous and concealed, dark-brown, scurfy and rugose
  - **3:** Peduncles terminal or axillary, all recurved, 1–20 mm long, shorter than subtending leaves; leaves narrowly ovate to ovate (*O. apicifolia* can be linear), sessile or petiolate; inflorescence either a simple or compound capitulum, infructescence either a capsular syncarpium or a capsiconum.
  - **6.** Twining climbers with weak trailing or climbing stems; plants more or less glabrous; leaves large (30–60 mm long), thin, distinctly petiolate; capitula large (3–5 florets per capitulum, 4–6 capitula per compound capitulum); stipules

6:

	long (5–10 mm) and recurved; seed rugose, mature seed usually with single, thick linear elaiosome covering the thin ventral keel, thin ridge on dorsal surface, ventra furrows broad	al
6:	Erect subshrubs or perennial herbs, not climbers; plants glabrous, scabrous or hirsute; combination of characters not as above	
7.	Leaves sessile or very shortly petiolate, with recurved or revolute margins; plant robust, stems stout and stiff	s
8	Leaves small (2–6 mm long), ovate, glabrous, coriaceous, with distinctly recurved to revolute margins. [seed not seen] (Nullarbor; coastal limestone cliffs)	O. loganioides
8	Leaves not as above, notably scabrous at least on upper surface and margins	
	9. Plants with glabrous to scabrous stems, leaves scabrous on upper surface and with thickened, scabrous and minutely recurved margins, stipules glabrous with ciliate margins, indumentum of papillae and short hairs (0.1–0.3 mm lor capsiconum (including corolla and calyx lobes) glabrous and not appearing echinate; seeds obovate in outline, dark brown and flecked with white, rugulose and scurfy, dorsal surface not rounded, sometimes cristate	ng);
	9: Plant densely and conspicuously hispid or setose; stems, stipules, leaves and flowers covered with long, stiff bristles (0.5–2.0 mm long), leaf margins distinctly hispid and recurved or revolute; capsiconum (including calyces) co stiff bristles, appearing echinate; seeds elliptic in outline, dark brown, dorsal surface rounded and smooth	
7:	Leaves distinctly petiolate (can be shortly petiolate) with flat to recurved margins; plants delicate, stems slender and flexible	
1	0. Leafy plants with sparsely to densely hirsute, pilose or villous stems and leaves leaves ovate to broadly ovate, or broadly obovate, highly variable in size, 10–40(–50) mm long; capitula simple or compound, with few (4–8) to many (15–>20) flowers; seed light brown, dorsal and ventral surfaces distinctly rugor ventral surface with two shallow furrows; elaiosome absent, seed edge not demarcated from seed body	se,
1	<b>0:</b> Almost leafless to few-leaved plants with glabrous or minutely scabrous stems and leaves; leaves narrowly lanceolate or linear, small, 5–15(–20) mm long; capitula simple with consistently few (3–5) flowers; seed dark brown, dorsal surface rounded and relatively smooth or slightly wrinkled, ventral surface wrinkled with two deep furrows and a single, thick, linear elaiosome obscuring the keel, and distinctive rim on seed edge	5

# Species notes, typifications and taxonomy

**Opercularia acolytantha** Diels, *Bot. Jahrb. Syst.* 35: 547 (1905). *Type citation*: 'Hab. in distr. Eyre a sinu Esperance Bay circ. 60km septentrionem versus in apertis aridus arenosis fruct. m. Novemb. (D. 5967).' (*holotype*: B *n.v.*, destroyed in WWII). *Type*: Mt Heywood, Western Australia [precise locality withheld for conservation reasons], 12 December 1992, *W.R. Archer* 1212926 (*neo*, here designated: MEL 2041551!).

Low, semi-woody, short-lived perennial *herb* or *subshrub*, (4-)5-10(-16) cm tall, with weak taproot 4-10(-13) cm long, suckering from lateral roots. *Stems* erect, arising singly or in multiples from base, simple or branched, glabrous to scabrous, ribbed-sulcate. *Leaves* opposite, simple, sessile to near-sessile,

leaf abscission zone absent, (4-)6-15(-20) mm long, (0.6-)1.0-2.5(-3.7) mm wide, length: width ratio 4–15, lamina concolorous, green with red apices, straight or falcate, linear, ensiform or narrowly ovate, minutely and sparsely scabrous to scabrous; apex acute-mucronulate; margins flat, entire; seedling leaves relatively larger, obovate and petiolate. Hairs short, stiff, straight, erect bristles c. 0.3 mm long, on leaves, calyx, ovary and (less frequently) stems and peduncles, papillae occasionally found on peduncles. Stipules interpetiolar, triangular-bifurcate, fused with leaf bases into prominent collar, red, becoming brown and scarious with age, +/- glabrous; lobes (1–)2–4, with apical colleters. *Inflorescence* a globular capitulum, 7-10 mm wide in flower, 4-8 mm wide in fruit, 15-30 flowers per capitulum, capitula often subtended by a pair of leaf-like bracts 1-6 mm long, occasionally secondary capitula arising on a peduncle emerging from the base of the primary capitulum. Peduncles 5-30(-50) mm long, erect in flower, further elongating during maturity and becoming decurved to strongly decurved in fruit, glabrous or (less frequently) scabrous. Flowers sessile on receptacle, separate from one another, bisexual or with female-only flowers, bisexual flowers protogynous, female flowers with staminodes. Calyx sparsely scabrous (occasionally glabrous), green, calyx tube adnate to ovary; lobes 5, becoming purple-tipped, unequal for the most part, 2 major (1.2–2.0 mm long) and 3 minor (0.6–1.1 mm long), ovate-triangular with acute apices, bearing a pair of minute denticles (<0.1 mm long) with apical colletors at base of each lobe. Corolla glabrous except for minute papillae on lobe margins, purple to cream or green; on female flowers tubular, barely exceeding calyx; tube 0.7–0.8 mm long; lobes 4 or 5, 0.2–0.8 mm long, on bisexual flowers campanulate, exceeding calyx; tube 0.4–1.0(–1.6) mm long; lobes 4 or 5, 0.7–1.0 mm long. Staminodes 4 per female flower, 0.3–0.4 mm long. Stamens 4, free to base of corolla; filaments 2.2–3.1 mm long at maturity, exserted 1.0–1.8 mm beyond corolla; anthers 0.9–1.6 mm long, cream-yellow with blue flecks, dehiscing by longitudinal slits, with apical process. Ovary inferior, scabrous, 0.8–1.0 mm long, uniloculate with single ovule, tubular to funnelform. Style 2.5–5.2 mm long, 1.0–4.0 mm exserted, bifid for 1/2–4/5 length, filiform, purple, papillose, papillae 0.20–0.25 mm long. Fruit a utricle encasing a single seed, unfused and separate from one another on capitulum, sessile on receptacle, indehiscent, (1.2-)1.5-2.6(-2.9) mm long, (0.8-)1.1-1.9 mm wide, triangular in outline, crowned by persistent calyx lobes 0.7–1.0 mm long, scabrous to sparsely hispid, becoming inflated and scarious with maturity. Seeds c. 1.4-2.0 mm long, 0.5-2.0 mm wide and (0.5–)0.7–0.9 mm tall, elliptic, obovate or obtriangular in outline, trigonous with two deep furrows on the ventral face forming lateral appendages around a ventral keel, surface dark brown with white flecks, rugulose and covered in short, scurfy hairs. (Figures 1C, 2A–G, 3)

Diagnostic features. Opercularia acolytantha is distinguished from other species by the combination of the following characters: flowers and fruit unfused and free from one another on a common receptacle, infructescence a globular capitulum on decurved, elongate peduncles, capitula lacking opercula, fruit shed as a single, indehiscent utricle, leaves linear and scabrous, leaf margins not revolute, seed with two lateral appendages often obscured by scurfy scales and lacking an elaiosome.

Other specimens examined. WESTERN AUSTRALIA: [localities withheld for conservation reasons] 12 Dec. 1992, W.R. Archer 1212921 (MEL); 24 Jan. 1993, W.R. Archer 2401936 (MEL); 25 Oct. 2001 G.F. Craig 5525 (PERTH); 16 Oct. 1968, N.N. Donner 3049 (PERTH); 16 Oct. 1968, Hj. Eichler 20293 (PERTH); 30 Oct. 1965, A.S. George 7032 (PERTH); 10 Nov. 2013, M. Hoggart 9/1113; 28 Oct. 1985, G.J. Keighery 7311 (PERTH); 24 Oct. 1991, G.J. Keighery 12558 (PERTH); 1 Oct. 2012, A.S. Markey & S. Dillon SR 9650 (PERTH); 1 Oct. 2012, A.S. Markey & S. Dillon SR 9651 (PERTH); 3 Oct. 1973 K. Newbey 3855 (PERTH); 6 Oct. 1986, K. Newbey 11249 (PERTH); 6 Nov. 1968, J.W. Wrigley s.n. (CANB).

*Phenology*. Flowering occurs in September and October, followed by fruiting from October to December. After a dry spell in the later winter of 2012, fruits were found to have aborted in a population near



Figure 2. Opercularia acolytantha. A – flowering and fruiting plant showing the habit (plant c. 15 cm tall); B – flowering simple capitulum with styles exserted from florets; some florets are unisexual, some are protogynous and bisexual; C – single, intact, indehiscent fruit and extracted seeds showing dorsal (d) and ventral (v) surfaces (W.R. Archer 1212936; MEL 2041551); D – dried bisexual floret in male phase that has separated from the capitulum; E – intact pickled female floret with part of perianth removed to show staminodes (arrowed); F – stipules; G – fruiting capitulum (M. Hoggart 9/1113); H – fruiting capitulum (capsiconum) of O. vaginata for comparison. Scale bars = 5 mm (B, H), 3 mm (G), 2 mm (F), 1 mm (C–E). Photographs by A. Markey.

South Stirling. Typical for the genus, the bisexual flowers of *O. acolytantha* have been observed to be protogynous, and both bisexual and unisexual (female) flowers have been observed on the same head. Capitula with flowers both bisexual and female or entirely female-only have been observed in a population near South Stirling, but capitula with male-only flowers were not observed in that population.

Distribution and habitat. Found in scattered localities between Mount Barker and north-east of Esperance, in southern Western Australia (Figure 4). Occurs on sandplains, sandy flats, sands overlying

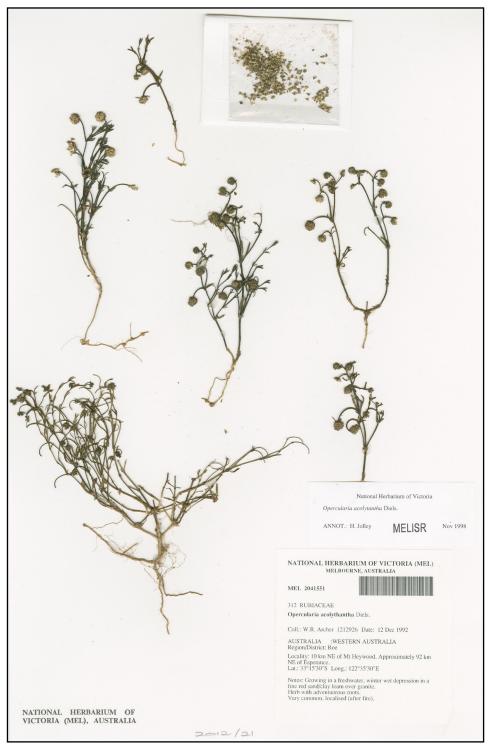


Figure 3. Neotype of *Opercularia acolytantha* (*W.R. Archer* 1212926; MEL 2041551). Reproduced with permission from the National Herbarium of Victoria (MEL), at the Royal Botanic Gardens Victoria.

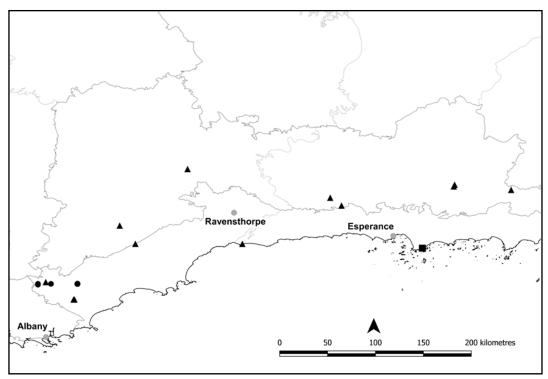


Figure 4. Distributions of *Opercularia hirsuta* (■), *O. acolytantha* (▲) and *O. nubicola* (●) in southern Western Australia. Only the one, most certain, location for *O. hirsuta* is mapped, as there are uncertainties as to the exact position of the other records for this species at Young and Oldfield Rivers and Esperance Bay.

laterite and clay, deep white sands and freshwater winter-wet sands over granite. Recorded from mallee and mallee-shrubland vegetation and coastal mallee-heath dominated by *Eucalyptus pleurocarpa* and *E. angulosa*, and in swamp yate (*E. occidentalis*) mallee.

Conservation status. Currently Nationally Listed as Extinct under the Environment Protection and Biodiversity Conservation Act 1999 (Department of the Environment and Energy 2018), and until 2018 listed in Western Australia as Extinct under Schedule 4 in the Wildlife Conservation Act 1950 (Western Australian Minister for the Environment 2015). The species was recently recognised as extant in Western Australia and listed as Priority Three (Smith 2018; Smith & Jones 2018) as a result of this study.

*Typification*. Neotypification is required since the holotype of *O. acolytantha* at B is presumed destroyed in the fire that followed a wartime bombing raid (Brown *et al.* 1998; Orchard 1999; Botanical Museum Berlin-Dahlem 2010) and no duplicate material has emerged to date. The neotype corresponds with the original description of the species and was collected close to the original locality.

Similar species. Collections of O. acolytantha have been previously misidentified either as O. rubioides or O. vaginata. In particular, O. vaginata and O. acolytantha can be easily confused because they share a similar growth form, similar linear to narrowly ovate leaves, globular capitula on elongate peduncles, and sulcate, glabrous or sparsely scabrous stems and peduncles. Together with O. liberiflora, O. acolytantha is distinguished from all other species of Opercularia by having flowers on the capitulum unfused and free. The fruits remain separate on the capitulum, lack opercula, are indehiscent,

become inflated at maturity and eventually fall from the receptacle (Figure 2). In comparison, the fused fruits of *O. vaginata* dehisce by opercula to release the seed (Figure 2). Both species have seed which lack elaiosomes and share the unusual seed character of two lateral appendages formed by deeply invaginated lateral furrows, but the seeds of *O. vaginata* are distinctly more obtriangular in outline (Figure 1). *Opercularia acolytantha* has strongly decurved and shorter fruiting peduncles as opposed to the elongate and erect fruiting peduncles of *O. vaginata*, and the capitula are 1–0.8 times the width of those of *O. vaginata* (Figure 2). Plants of *O. acolytantha* tend to be relatively short in height (5–10 cm tall) and are more sparsely stemmed than *O. vaginata*, which can grow to a height of 10–30 cm and form sparsely-stemmed to dense, bushy subshrubs or robust perennial herbs.

Notes. Prior to this current investigation PERTH had no collections identified as O. acolytantha. As the species was known from a single specimen (the type), the species has been listed as presumed extinct by both Western Australian and Federal authorities (Brown et al. 1998; Walter & Gillet 1998; Hopper et al. 1990; Craig & Coates 2001; Department of the Environment and Energy 2018). Despite five collections at either CANB or MEL being redetermined or confirmed as O. acolytantha within the past 40 years, neither typification nor reassessment of the conservation status of this species had been attempted before this current study. A search of material at PERTH and MEL has located several collections which fit the description of O. acolytantha by Diels (Diels & Pritzel 1904–5). This species is assumed to have been overlooked in collections and field studies for three reasons: there is no type for reference, it is a short-lived perennial, and it is morphologically similar to and easily confused with O. vaginata. Opercularia acolytantha is difficult to observe as plants grow and flower only within 1–3 years after fire. Sterile plants potentially of this species were located within one year after fire at a recollection site in the Stirling Range, but flowering plants were found 2–3 years after fire at another location south of the Stirling Range. Observations recorded on herbarium sheets (MEL 2041551, MEL 2041553) note that populations are common after fire, and transition from being locally common to completely absent from sites within two years after being first sighted (MEL 2041552).

Atypically for the genus, the fruit of *O. acolytantha* becomes a dry, scarious and inflated utricle at maturity (Figure 2). The seed is retained within the indehiscent fruit, which readily detaches from the receptacle and is assumed to be shed in its entirety as a diaspore. These relatively light-weight diaspores may be dispersed by wind or surface rainwater runoff to some degree, or the rigid and even-hooked calyx lobes may even facilitate ectozoochorous dispersal. Although lacking the elaiosome found on the seed of the presumably myrmecochorous species *O. echinocephala*, *O. volubilis* and *O. nubicola* (Figure 1) (Berg 1975; Lengyel *et al.* 2009), seed-harvesting ants or other animals may disperse these after they fall from the capitulum. More field observations are required to verify these postulates and to determine both the distances and means by which fruit are dispersed and seed liberated from the indehiscent fruit.

The vernacular name of this species is Esperance Dog Weed.

**Opercularia hirsuta** Benth., *Fl. Austral.* 3: 434 (1867). *Type citation*: 'Lucky Bay, Oldfield and Young rivers, Esperance Bay, *Maxwell'*. *Type specimens*: Lucky Bay [Western Australia], *s. dat.*, *G. Maxwell s.n.* (*syn*: MEL 2296181!; K 000772252 image!); Oldfield and Young River, Esperance Bay [Western Australia], *s. dat.*, *G. Maxwell s.n.* (*syn*: MEL 2296180!).

Erect *subshrub* or perennial, weakly or semi-woody *herb*, *c*. 30–50 cm tall. *Stems* virgate, sulcate, villose; *hairs* simple, non-septate, 2.5–3.0(–3.5) mm long, sometimes twisted, soft, almost silky. *Leaves* few on stems, opposite, simple, sessile, leaf abscission zone not evident, villose, 14–16(–19) mm

long, 2.0–3.5(–4.5) mm wide, length: width ratio 4–7, straight, linear or narrowly obovate; apex acute to obtuse; margins entire, flat, thick but not recurved; midrib visible abaxially (may be obscured by hairs), obscure adaxially; lateral veins obscure or absent. Stipules interpetiolar, fused with leaf bases into prominent collar, obscured by villose hairs; denticles 1 or 2 major and 0-2 minor, with apical colleters. Inflorescence a globular compound capitulum of several fused capitula, each capitulum with 4-6 fused florets, 15-25 florets per compound capitulum, 7-9 mm wide in late flower and early fruit, subtended by a pair of leaf-like, linear bracts 5–10 mm long. *Peduncles* erect in both flower and fruit, (7–)15–30(–60) mm long. Flowers fused to one another, sessile on common receptacle, bisexual, protogynous. Calyx densely hairy, 2.3–2.5 mm long; lobes 5, narrowly triangular with acute apex, equal, 0.5 mm long on mature, male-phase florets, shorter on younger, female-phase florets. Corolla densely hairy on abaxial surface, glabrous adaxially, free, starting as tubular and becoming urceolate in later developmental stages, exceeding calyx; tube 2.3–2.4 mm long; lobes 4–5, 0.7–0.9 mm long. Stamens 4 or 5, barely exserted beyond corolla; filaments c. 2.0–2.5 mm long, inserted at base of corolla; anthers 1.5–2.0 mm long, with apical process, dorsifixed, longitudinally dehiscent. Style deeply bifid, filiform, papillose, 3.0–3.5 mm long, exserted from corolla by 1.5–2.0 mm. Ovary inferior, villose, unilocular, one ovule per locule, fused to adjacent ovaries. Fruit a globular capsiconum of several (c. 3–6) fused syncarpia, each capsular syncarpium dehiscing by an operculum, covered with persistent calyx lobes 1.0–1.2 mm long, densely hairy. Seeds 2.0–2.3 mm long, 0.5–0.7 mm wide, narrowly obovate or narrowly elliptic in outline, with two ventral furrows, one on either side of a ventral keel, appearing bisulcate, glabrous, rugulose to tuberculate, light brown, covered in white flecks. (Figures 1A, 5, 6)

*Diagnostic features. Opercularia hirsuta* is distinguished from other species by having the combination of an elongate, erect peduncle subtending globular inflorescences, fused florets, a dense, villous indumentum covering stems, leaves, flowers and fruit, sessile, linear or narrowly obovate leaves, and bisulcate, fusiform seeds lacking an elaiosome.

*Specimens examined.* The description is based on examination of type gatherings and Bentham's original description. No specimens matching this description have been found at PERTH.

*Phenology*. The Maxwell specimens are in flower and fruit, but no information is provided which indicates the season during which they were collected. If these specimens were collected when Maxwell accompanied the Dempster brothers on their expedition from Albany to Point Culver in 1863, the timing of collection would have been between May and June (Anon. 1863).

Distribution and habitat. Restricted to the Esperance IBRA region of south-eastern Western Australia (Figure 4). Locations given are Lucky Bay, Oldfield River, Young River and Esperance Bay. Little information was given on Maxwell's collections except 'moist flats' and 'on banks of a small brook', which suggests *O. hirsuta* may occupy riverine habitats or freshwater seeps into sandy substrates adjacent to beaches or rivers. Recent attempts failed to locate this species at Cape Le Grand along the banks of a small freshwater creek (Markey 2012), and along the lower reaches of the Oldfield River estuary.

Conservation status. Opercularia hirsuta is currently listed in Western Australia as a poorly known species with Priority Two conservation status (Smith & Jones 2018). An examination of all Opercularia collections at PERTH and MEL has failed to find any collections which match the syntypes held at K and MEL. Opercularia hispidula has been commonly mistaken for O. hirsuta, which has led to overestimations of the range and population size of O. hirsuta. Because this species has not been

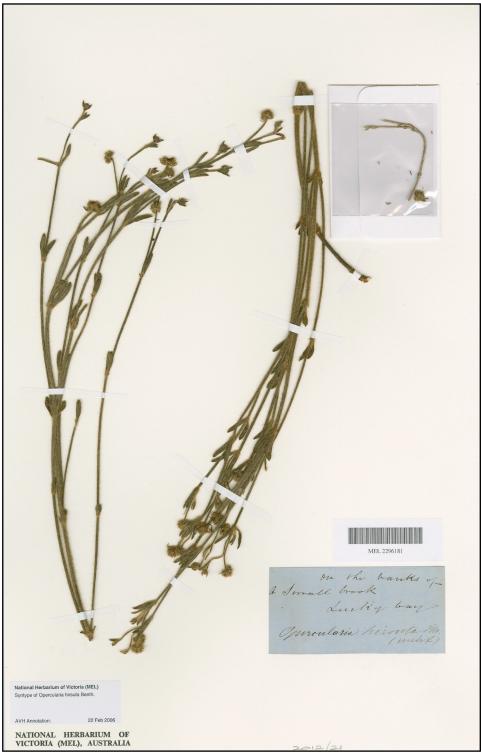


Figure 5. Syntype of *Opercularia hirsuta* (*G. Maxwell s.n.*; MEL 2296181). Reproduced with permission from the National Herbarium of Victoria (MEL), at the Royal Botanic Gardens Victoria.

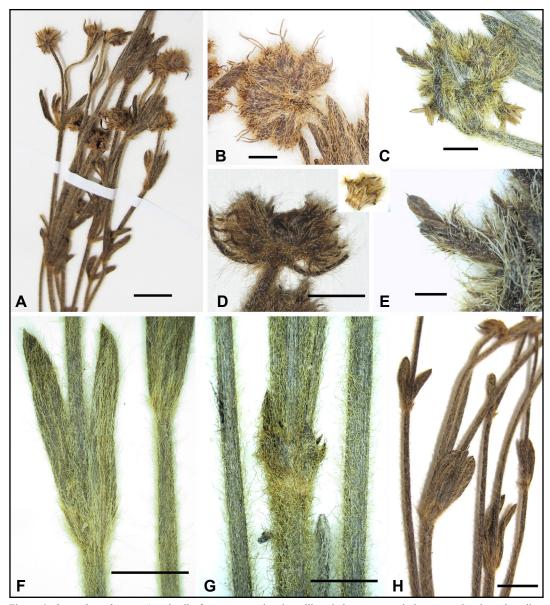


Figure 6. Opercularia hirsuta. A – detail of erect stems showing villose indumentum and elongate peduncles subtending compound capitula; B – capitulum with florets in female phase with exserted styles; C – compound capitulum in male phase showing barely exserted anthers; D – capsiconum showing dense indumentum and detached operculum from one of the capsular syncarpia (insert); E – detail of male phase floret showing anthers and corolla; F – detail of leaves; G – detail of interpetiolar stipule and stem; H – detail of stem and leaves. Scale bars = 10 mm (A, H, F), 5 mm (D, G), 2 mm (B, C), 1 mm (E). Images from G. Maxwell S.R. (MEL 2296181). Reproduced with permission from the National Herbarium of Victoria (MEL), at the Royal Botanic Gardens Victoria. Photographs by E. Markey.

recollected since the original 1863 expedition of Maxwell along the south coast, it is possible that *O. hirsuta* is rare and threatened, perhaps even extinct. It is a species requiring both further field survey and examination of other herbarium collections to assess its conservation status.

Similar species. Many of the collections previously identified as O. hirsuta at PERTH were actually O. hispidula. Most of these misidentified collections were the coastal or granite outcrop ecotypes

with coriaceous and densely hirsute to villous leaves (Figure 7). The crucial difference between these two taxa is the length, shape and position of the peduncle. *Opercularia hirsuta* has an elongate, erect peduncle and sessile, linear or narrowly obovate leaves with acute to obtuse apices (Figures 5, 6), whereas *O. hispidula* has a short, pendulous and recurved peduncle and distinctly petiolate, narrowly obovate to obovate leaves with acute or acuminate apices (Figure 7). Both species have brown, rugulose to rugose, bisulcate seeds lacking an elaisosome, but the seeds of *O. hirsuta* are flecked with white, and narrowly obovate to narrowly elliptic, whereas those of *O. hispidula* are obovate- to elliptic, markedly rugose and uniformly light brown (Figure 1). The two species can share a similar habit, although subshrubs of *O. hispidula* vary from prostrate and compact to fewbranched, erect and flexuose.

The vernacular name of this species is Silky-haired Stinkweed.

# Opercularia nubicola A.S.Markey, sp. nov.

*Type*: Stirling Range National Park, Western Australia [precise locality withheld for conservation reasons], 1 March 2015, *A. Markey & S. Dillon* SR 9653 (*holo*: PERTH 08772754; *iso*: CANB, MEL).

*Opercularia* sp. Stirling Range (M. Hislop 2839), Western Australian Herbarium, in *FloraBase* https://florabase.dpaw.wa.gov.au/ [accessed 2 June 2017].

[Opercularia rubioides auct. non Juss.: G. Bentham, Fl. Austral. 3: 435 (1867).]

An erect, tufted, leafy perennial herb or subshrub c. 30–60 cm tall. Stems erect, wiry, branches arising from stout, short, woody base, young stems glabrous (occasionally scabrous), minutely sulcate, resinous, older stems becoming brown and scarious; indumentum of both papillae and short, stiff hairs, these 0.1–0.3 mm long, conical, uncinate or straight, ascending or adpressed. *Leaves* opposite-decussate, connate at interpetiolar stipule and oriented parallel to stem, sessile to very shortly petiolate; petiole 0-1.5 mm long; lamina 12-26 mm long, 4-6 mm wide, concolorous, bright green, narrowly ovate, coriaceous, rigid, distinctly scabridulous or scabrous adaxially, surface becoming resinous, abaxial surface glabrous; apex acute with prominently rigid tip; margins entire, thickened, scabridulous or scabrous and minutely recurved (particularly on dry material); lateral veins several, raised on abaxial surface and visible on adaxial surface. Stipules fused into an interpetiolar stipule, glabrous to (less frequently) sparsely scabrous, stipule margins often sparsely ciliate with stiff, ascending hairs, green, fleshy with 1-2(-3) triangular lobes. *Inflorescence* a spherical compound capitulum of 2-4 (usually 3) fused capitula, often subtended by several involucral bracts, each capitulum with 3–5 fused florets, 10–20(–25) florets per compound capitulum, compound capitulum 7–10 mm diam. Peduncles short and recurved or nearly sessile on both terminal and axillary capitula, 1.5–4.0(–7.0) mm long. Flowers bisexual, connate on a common receptacle. Calyx narrowly triangular, glabrous or minutely scabrous on margins, lacking hairs, persistent on fruit; lobes 3-5, 3-5 mm long in flower, 1.5-3.0 mm long in fruit, linear to narrowly triangular with acute apex. Corolla urceolate in female phase, becoming tubular with anther exsertion, 3.0–3.5 mm long; tube 1–2 mm long; lobes 4, 0.8–1.0 mm long with obtuse to acute apices, glabrous. Stamens 4; filaments inserted at base of corolla, 3.5-4.5 mm with 1–2 mm exserted from the corolla; anthers yellow or blue, (1.0–)1.5–2.0 mm long, longitudinally dehiscent, dorsifixed. Ovary inferior, glabrous, uniloculate or biloculate with one ovule aborted, fused to ovaries of adjacent flowers. Style deeply bifurcate, purple, papillose, 5 mm long with 2.5 mm exserted from the corolla. Fruit a globular capsiconum of 2–4 syncarpia, each individual syncarpium capsular and dehiscing by an operculum, 7–9 mm diam., glabrous to scabrous, not subtended by bracts.

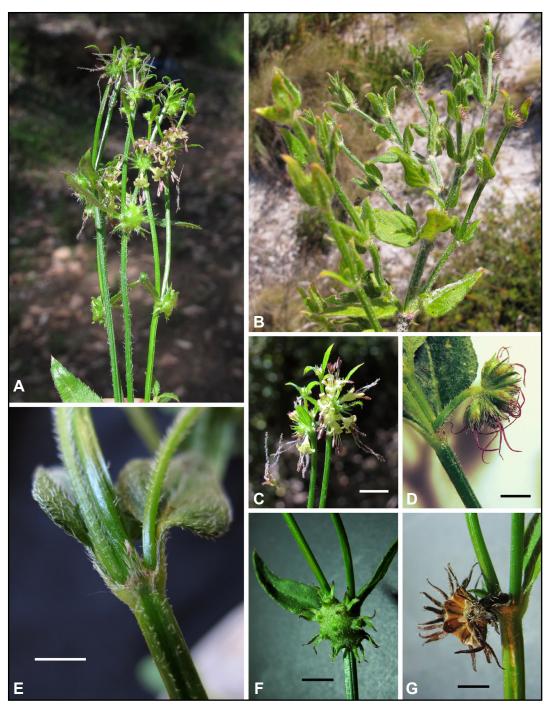


Figure 7. Features of *Opercularia hispidula*. A – erect stems *in situ* showing sparse indumentum and short, decurved peduncles subtending capitula in a few-flowered form (Porongurup National Park); B – coastal ecotype *in situ* with thick, broad leaves (Cape Le Grand National Park); C – compound capitulum in male phase showing distinctly exserted anthers; D – compound capitulum in female phase showing long-exserted styles; E – detail of interpetiolar stipule and stem; F – immature capsiconum; G – dehisced capsiconum, showing star-shaped cavity remaining after loss of operculum and seeds. Scale bars = 5 mm (C), 3 mm (E, F), 2 mm (D, G). Photographs by E0. Markey.

Seeds 1.3–2.0 mm long, 0.6–0.8 mm wide, 0.5–0.7 mm high, obovate to elliptical, trigonous, dark brown flecked with white, rugulose, sometimes cristate on dorsal face, with a keel formed between two broad furrows on ventral face and flanked on either side by an elaiosome. (Figures 1, 8)

*Diagnostic features.* Distinguished from other Western Australian species by the combination of markedly sessile or near-sessile, narrowly ovate, rigid, coriaceous leaves, tapering to an acute apex with a rigid, pointed tip, rugulose obovate to elliptical seed with a pair of elaiosomes bordering a ventral keel bordered by two broad furrows.

Other specimens examined. WESTERN AUSTRALIA: [localities withheld for conservation reasons] 18 Oct. 1994, S. Barrett 47 (PERTH); 6 Dec. 1994, S. Barrett 141 (PERTH); 7 July 1985, E.J. Croxford 4312 B (PERTH); 1849, J. Drummond 435 (MEL, P); 20 Oct. 2002, M. Hislop 2839 (PERTH); 1 Mar. 2015, A.S. Markey & S. Dillon SR 9654–9656 (all PERTH); 12 Mar. 2015, D.A. Rathbone DAR 991 (PERTH).

Phenology. Flowering July-November (peaking around October), with mature capitula shedding seed from February-March.

Distribution and habitat. Restricted to the quartzite peaks of the Stirling Range in southern Western Australia (Figure 4), where it grows in shallow brown loams on rocky substrates, including rock cervices, vertical surfaces and beneath overhangs (Figure 8). Growing in open heath and low *Eucalyptus* woodland. Associated species: *Kunzea montana*, *Acacia drummondii*, *Hakea florida*, *Banksia formosa*, *Nemcia rubra*, *Eucalyptus megacarpa*, *Corymbia calophylla*, *Calothamnus montanus* and *Xanthosia rotundifolia*.

Conservation status. Opercularia nubicola is listed by Smith and Jones (2018) as Priority Two under Conservation Codes for Western Australian Flora, under the name O. sp. Stirling Range (M. Hislop 2839). It has a limited distribution within a single national park and its montane habitat is vulnerable to fire, dieback and both rainfall decline and temperature extremes predicted to occur with climate change (Barrett & Yates 2015).

Etymology. From the Latin *nubicolus* (cloud-dwelling), this species is named after the cloudy, montane habitat in which it resides, and is inspired by the Noongar name for the Stirling Range, *Koi Kyenunu-ruff*, which describes mountain peaks enshrouded in rolling mist.

Affinities. There are no other species of Opercularia in Western Australia that are closely allied to O. nubicola. Although greatly disjunct from eastern Australian, it is closely allied to O. aspera by its scabrous, coriaceous leaves and overall seed and capitulum morphology. Opercularia aspera is a highly variable entity comprised of forms that were originally described as separate taxa by Gaertner (1788), Young (1797), Jussieu (1804) and Sprengel (1825), which were later synonymised or reduced to varietal status by Bentham (1867) (see notes below on O. rubioides). Following careful examination, a combination of characters were identified which distinguished O. nubicola from O. aspera s. lat., as follows (also presented in Table 1 for clarity). Opercularia nubicola is distinguished from O. aspera by the combination of sessile to very shortly petiolate leaves, shortly scabrous or scabrous indumentum on adaxial leaf surfaces only, glabrous abaxial leaf surfaces, glabrous or minutely scabrous calyces on the capsiconum, longer and broader calyx lobes, fewer capitula per compound capitulum, fewer florets per compound capitulum, and longer capitulum bracts.



Figure 8. *Opercularia nubicola*. A – fruiting plant, *in situ* on fractured bedrock displaying the erect, subshrub growth habit; B – stems, showing coriaceous, sessile leaves; C – inflorescences on dried specimen, showing globular, flowering, compound capitula; D – mature capsiconum on a short peduncle; E – leaf adaxial leaf surface showing scabrous surface; F –interpetiolar leaf stipule, showing bifurcation into two lobes capped by apical denticles. Scale bars = 10 mm (D), 2 mm (E, F). Images from *A.S. Markey & S. Dillon* SR 9653 (A), *A.S. Markey & S. Dillon* SR 9656 (B, D–F) and *M. Hislop* 2839 (C). Photographs by A. Markey (A, B, D–F) and S. Dillon (C).

Similar species. Sometimes confused with O. volubilis, O. nubicola can be distinguished by its erect, shrubby habit, coriaceous, scabrous leaves with a distinctive sandpapery texture, whereas O. volubilis is a glabrous climber or twining shrub with smooth, relatively thin leaves. The stipules of O. volubilis are flexuose, two-lobed and decurved from the node as opposed to being erect and adpressed to the stem in O. nubicola. Opercularia nubicola can also be confused with O. hispidula (Figure 7), the latter species having soft, thin leaves and distinctly hirsute, pilose or villous leaves, flowers and stems, as opposed to the scabrous, coriaceous and distinctly acute, rigid-tipped leaves of O. nubicola (Figure 8). Opercularia echinocephala may also be mistaken for O. nubicola, but this species has a distinctly hispid or setose indumentum composed of longer (>0.5 mm) hairs. Differences in seed morphology among Western Australian species are illustrated in Figure 1. Both O. volubilis and O. apicifolia Juss. have a single elaiosome covering the ventral keel, whereas both O. nubicola and O. echinocephala have the elaiosome on either side of this ventral keel. The seeds of O. hispidula are lighter brown, distinctly rugose, lacking an elaiosome, shorter in length and more elliptic in shape than for O. nubicola.

The suggested vernacular name is Stirling Range Stinkweed.

Table 1. Comparison of morphological traits between Opercularia nubicola and O. aspera s. lat.

Character	O. nubicola	O. aspera s. lat.
Calyx lobes lengths (mm)	3–5 in flower 1.5–3.0 in fruit	1.5–2.7 in flower (0.6–)1.0–2.5(–3.0) in fruit
Calyx lobe and involucral bract (if present) shape and position relative to florets	Long and broad. Noticeably longer than the corolla. Characteristically enclosing and extending beyond the florets	Short and narrow. Not enclosing or extending beyond florets
Counts of individual capitula / capsular syncarpia per compound capitulum / capsiconum	2–4 (usually 3)	5–7
Florets per compound capitulum	10–20(–25)	20–35(–40)
Leaf shape	Narrowly ovate, apex acute	Narrowly ovate, ovate or elliptic, apex acute, mucronate or mucronulate
Stem and leaf indumentum	Consistently scabrous on leaves. Usually glabrous stems and glabrous stipules with hairs on margins, but these can be shortly scabrous or scabrous	Ranging from glabrous, scabrous, strigose to densely hispid on leaves, stems and stipules
Petiole presence / length	Leaves consistently near-sessile or sessile (petiole 0–1.5 mm)	Leaves ranging from sessile or near- sessile (petiole 0.5(-1.0) mm) to distinctly petiolate (petiole 2–5 mm)
Calyx and fruiting capitulum indumentum	Usually glabrous, occasionally sparsely scabrous (hairs mostly restricted to the calyx margins)	Can be glabrous (as observed in the 1770 Banks and Solander collections from Port Jackson) but are more commonly scabrous or hispid, often densely so
Hair lengths and shape	Hairs are short (0.1–0.3 mm ), stiff, conical, curved or straight	Hairs range from short (0.1–0.3 mm) to longer (0.5–0.7 mm), and vary in shape from flattened and triangular to pointed, conical, curved or straight

## Species excluded from Western Australia

**Opercularia aspera** Gaertn., *Fruct. Sem. Pl.* 1: 112, t. 24, Fig. 4 (1788). *Type*: 'Ex herbario Banksiano, Habitat in Neo-Selandia'. (*syn*: MEL 2268202!, MEL 2268203!, MEL 2268204!, P 03980241 image!, P 03980244 image!, P 03981519 image!, BM 001040395 image!).

Opercularia hyssopifolia Juss., Ann. Mus. Natl. Hist. Nat. 4: 428, t. 71, Fig. 1 (1804). Opercularia aspera var. hyssopifolia (Juss.) Benth., Fl. Austral. 3: 434 (1867). Type: 'In Australasiâ. Car. ex siccâ vix fructiferâ quam a D. Née acceptam communicavit D. Thibaud.' (syn: MPU 014131 image!).

Opercularia ligustrifolia Juss., Ann. Mus. Natl. Hist. Nat. 4: 428, t. 71, Fig. 2 (1804). Opercularia aspera var. ligustrifolia (Juss.) Benth., Fl. Austral. 3: 434 (1867). Type: 'Car. ex siccâ fructifera ab eodem D. Thibaud communicatâ.' (syn: ? P 03911644 image!).

Opercularia rubioides Juss., Ann. Mus. Natl. Hist. Nat. 4: 428 (1804), syn. nov. Type citation: 'In Australasiâ. Car. ex siccâ in Musaei herbaris nuperrimè observatâ et ideò non delineatâ.' Type specimen: Port Jackson, Nouvelle Hollande Côte orientale, [1802], Baudin expedition 40 (lecto, here designated: P 03981579 image!; syn: G-DC G00667896 image!).

Notes. Opercularia rubioides was first recognised as occurring in Western Australia by Bentham (1867: 435), who referred a collection by James Drummond (5<sup>th</sup> Coll., n. 435) to this species, noting that it 'accords better with Jussieu's character, especially as the sessile leaves, than any of the forms of O. aspera'. Bentham considered O. rubioides restricted to Western Australia, a notion that has been followed to the present day (Western Australian Herbarium 1998–; CHAH 2006–); however, this circumscription is at odds with the type gathering of O. rubioides, which was collected in southeastern Australia.

Jussieu's herbarium and types are at the Muséum National d'Histoire Naturelle (P; Stafleu & Cowan 1979: 477–478). Although Jussieu (1804) described O. rubioides from material held at the time at P, he did not specifically cite any specimens, only indicating that the distribution was in Australasia. Following examination of collection images via the P Catalogue of Herbarium specimens, it appears that the only specimens of O. rubioides and allied species available to Jussieu in or prior to 1804 were the collections of Banks and Solander, the Née collections from Thibaud's herbarium and those collected on Baudin's 1801-1804 expedition aboard Le Naturaliste and Le Géographe. Baudin's expedition stayed in Port Jackson (Sydney) from May-November 1802 (Duyker 2006; George 2009) after exploring parts of the coastline of Australia and Timor. The first allotment of material collected on this expedition was dispatched from Port Jackson in November 1802 on board Le Naturaliste, including eastern Australian collections of the O. aspera alliance, arriving in Paris in June 1803 (Duyker 2006). Later collections from the expedition's further travels, including a second exploration of the southern Western Australian coastline, arrived in Paris in March 1804 with the return of the remainder of the expedition aboard Le Géographe and Le Casuarina (Duyker 2006). This second allotment was most likely too late for inclusion in Jussieu's December 1804 publication. Among the collections annotated as O. rubioides currently held at P of a suitable date and location to possibly be the type for O. rubioides is the sheet P 03981579 (only scans available online have been seen by author). The writing affixed to the sheet, which appears to be that of Leschenault, indicates that it was collected from 'Port Jackson' and the pre-printed label indicates it was collected on the eastern coast of New Holland by the Baudin Expedition in 1801 [1802] (Jangoux 2010). Consequently the sheet P 03981579 cited above is considered to be type material of O. rubioides. De Candolle (1830) states that he was sent material of this species from P and refers to its occurrence in eastern Australia. There is a presumed extant duplicate of the type in de Candolle's herbarium at Geneva (G-DC G 00667896); the P specimen has been chosen as the lectotype because it has the strongest provenance.

The type of *O. rubioides* has been determined here as referable to the earlier-named *O. aspera*, a widespread and variable species from Queensland, New South Wales and Victoria (James & Allen 1992; Jeanes 1999; CHAH 2006–). *Opercularia rubioides* is therefore treated as a synonym of *O. aspera* and should be removed from Western Australia's vascular plant census and from the *Threatened and Priority Flora list for Western Australia* (Smith & Jones 2018).

Because *O. nubicola* is restricted to an inland mountain range in southern Western Australia, it was not encountered until the 1840s when it was first collected by Drummond (5<sup>th</sup> Coll., *n.* 435) and misapplied to *O. rubioides* by Bentham (1867). With the exception of *Drummond* n. 435, Western Australian collections previously identified as *O. rubioides* have been found to be referable to either *O. acolytantha*, *O. vaginata* or *O. echinocephala*. However, several PERTH collections (previously unidentified or misidentified as *O. volubilis*) are a close match to Drummond's collection and Bentham's description of *O. rubioides*, all of which come from a limited area in the uplands of the Stirling Range in far south-western Western Australia. Although the exact location is absent from his specimen, Drummond is also known to have collected in the Stirling Range as part of his 5<sup>th</sup> Collection (Barker 2005; Maslin & George 2005). These collections are attributable to *O. nubicola*.

**Opercularia scabrida** Schltdl., *Linnea* 20: 604 (1847). *Type specimen*: An steinigen Orten in Scrubgegenden, South Australia, '90', 1844–1845, *H.H. Behr s.n.* (holo: HAL 0098342).

Although *O. scabrida* is currently listed in the Western Australian plant census (Western Australian Herbarium 1998–), Bentham (1867) noted this species was restricted to eastern Australia. Because no collections held at PERTH have ever been identified as *O. scabrida*, nor match either its description (Bentham 1867; Toelken 1986; Jeanes 1999) or representative accessions loaned from the eastern States, it is considered here as absent from Western Australia. Examination of two Western Australian collections identified as *O. scabrida* and held at MEL found these to be either *O. spermacocea* Juss. (MEL 2267542), *O. vaginata* (MEL 2267542) or *O. acolytantha* (MEL 2267541). Specimens collected by R. Helms on the Elder Exploring Expedition and identified as *O. scabrida* (albeit with a note of shorter peduncles than usual) in the expedition report (Mueller & Tate 1896) are apparently the basis of the Western Australian record for this species. The individual mounted on the top left of MEL 2267542 is referable to *O. spermacocea* while the individual mounted on the bottom left of the sheet is referable to *O. vaginata*.

## Acknowledgements

The curation staff at the Western Australian Herbarium (PERTH) are graciously thanked for their continued support, in particular Julia Percy-Bower, Skye Coffey, Meriel Falconer, Karina Knight, Evelyn McGough and Cheryl Parker. Many thanks are extended to the staff of the National Herbarium of Victoria (MEL) and Australian National Herbarium (CANB) for the provision of loans and digitised sheet images, and to MEL and staff members Wayne Gebert and Josephine Milne, for supporting my visit. Adrian Pinder and Kirsty Quinlan (Department of Biodiversity, Conservation and Attractions) are thanked for providing access to their microscopes and imaging software. Laurence Loze and Laurent Gautier (Herbarium of the Conservatoire botanique de la Ville de Genève) are thanked for providing digitised images of Opercularia specimens used for the preparation of de Candolle's Prodromus (G-DC). Melanie Smith and Sarah Barrett (Department of Biodiversity, Conservation and Attractions) are thanked for their help with site and population information and addressing the conservation statuses of these species. I am deeply indebted to Juliet Wege, Terry Macfarlane, Mike Hislop, Ryonen Butcher, Kevin Thiele and an anonymous reviewer for providing generous guidance on both this manuscript and the perplexing taxonomic issues which arose in such a long-neglected genus. Particular acknowledgment is given to Steve Dillon (PERTH) for his expertise and support in the field and herbarium.

#### References

Anon. (1863). Journal of an expedition to Point Culver, in the Australian Bight. *The Inquirer and Commercial News*, Wednesday 23 September 1863, p. 3. https://trove.nla.gov.au/newspaper/article/66013713 [accessed 8 February 2018].

Barker, R. (2005). James Drummond's plant collections today – a global dispersal. *In*: Davies, S.J.J.F. (ed.) *The Drummond Symposium: A review of the work of James Drummond, the first Government Botanist in Western Australia.* Symposium held at Toodyay, Western Australia, by the Toodyay Naturalist's Club, August 27th 2004. *Curtin University of Technology, Department of Environmental Biology Bulletin* no. 27. pp. 40–57.

Barrett, S. & Yates, C.J. (2015). Risks to a mountain summit ecosystem with endemic biota in southwestern Australia. *Austral Ecology* 40: 423–432.

Bentham, G. (1867). Flora Australiensis. Vol. 3. (Reeve and Co.: London.)

Berg, R.Y. (1975). Myrmecochorous plants in Australia and their dispersal by ants. *Australian Journal of Botany* 23: 475–508. Blackall, W.E. & Grieve, B.J. (1982). *How to know Western Australian wildflowers* (2<sup>nd</sup> edition). Part IV. (University of Western Australia Press: Nedlands, Western Australia.)

- Botanical Museum Berlin-Dahlem (2010). List of families including extant collections of the Botanical Museum Berlin-Dahlem (B) from the time before 1943. http://www.bgbm.fu-berlin.de/BGBM/research/colls/herb/phanerog.htm [accessed 15 November 2012].
- Brown, A., Thomson-Dans, C. & Marchant, N. (1998). Western Australia's Threatened flora. (Department of Conservation and Land Management: Como, Western Australia.)
- Candolle, A.P. de (1830). Prodromus systematis naturalis regni vegetabile. Vol. 4. p. 616. (Treuttel & Würz: Paris.)
- Council of Heads of Australasian Herbaria (2006–). *National Species List*. Available on https://biodiversity.org.au/nsl/services/[accessed September 2017].
- Craig, G.F. & Coates, D.J. (2001). *Declared rare and poorly known flora in the Esperance district*. Wildlife Management Program No. 21. Report to Department of Environment and Conservation. (Department of Environment and Conservation: Kensington, Western Australia.)
- Department of the Environment and Energy (2018). Threatened Species and Ecological Communities, EPBC Act (1999) List of Threatened Flora. http://www.environment.gov.au/cgi-bin/sprat/public/publicthreatenedlist.pl?wanted=flora [accessed 8 February 2018].
- Diels, F.L.E. & Pritzel, E. (1904–5). Fragmenta Phytographiae Australiae occidentalis: Beiträge zur Kenntnis der Pflanzen Westaustraliens, ihrer Verbreitung und ihrer Lebens-Verhältnisse. *Botanische Jahrbucher fur Systematik* 35: 293.
- Duyker, E. (2006). François Péron-An impetuous life: naturalist and voyager. (Miegunyah Press: Carlton, Victoria.)
- Gaertner, J. (1788). De fructibus et seminibus plantarum. Vol. 1. (Typis Academiae Carolinae: Stuttgart.)
- George, A.S. (2009). Australian botanist's companion. (Four Gables Press: Kardinya, Western Australia.)
- Hewson, H.J. (1988). Plant indumentum: a handbook of terminology. (Australian Government Publishing Service: Canberra.)
- Hopper, S.D., van Leeuwen, S., Brown, A.P. & Patrick, S.J. (1990). Western Australia's Endangered Flora and other plants under consideration for declaration. (Department of Conservation and Land Management: Wanneroo, Western Australia.)
- James, T.A. & Allen, W.K. (1992). Opercularia. In: Harden, G.J. (ed.) Flora of New South Wales. Vol. 3. pp. 490–492. (New South Wales University Press: Kensington, New South Wales.)
- Jangoux, M. (2010). The herbarium of the *Terres Australes* (Baudin Expedition, 1800–1804). http://sydney.edu.au/arts/research/baudin/pdfs/herbarium/H0-Introduction-Baudin%20herbarium.pdf [accessed 12 February 2018].
- Jeanes, J.A. (1999). Rubiaceae. In: Walsh, N.G. & Entwisle, T.J. (eds) Flora of Victoria. Vol. 4, Cornaceae to Asteraceae. pp. 616–642. (Inkata Press: Melbourne.)
- Jussieu A.-L. de (1804). Mémoire sur l'*Opercularia*, genre de plantes voisin de la famille des Dipsacées. *Annales du Mus*éum *National d'Histoire Naturelle* 4: 416–428.
- Keighery, G.J. (1999). A new species of Opercularia (Rubiaceae) from Western Australia. Nuytsia 13(1): 29-32.
- Lengyel, S., Aaron, D., Gove, A.D., Latimer, A.M., Majer, J.D. & Dunn, R.R. (2009). Ants sow the seeds of global diversification in flowering plants. *PLoS ONE* 4(5): e5480. doi:10.1371/journal.pone.0005480.
- Markey, A.S. (2012). A targeted spring flora survey of New Island Bay, Cape Le Grand National Park. Unpublished report prepared for Tourism Branch, Department of Environment and Conservation. (Department of Environment and Conservation: Kensington, Western Australia.)
- Maslin, B.R. & George, A.S. (2005). James Drummond's collections from south-west Western Australia. In: Davies, S.J.J.F.
   (ed.) The Drummond Symposium: a review of the work of James Drummond, the first Government Botanist in Western Australia. Symposium held at Toodyay, Western Australia, by the Toodyay Naturalist's Club, August 27th 2004. Curtin University of Technology, Department of Environmental Biology Bulletin no. 27. pp. 34–39.
- Mueller, F.J.H. von (1863-4). Fragmenta phytographiae Australiae. Vol 4. (Government Printer: Melbourne.)
- Mueller, F.J.H. von & Tate, R. (1896). Phanerogams and vascular cryptogams. Transactions of the Royal Society of South Australia 16(3): 333–383.
- Orchard, A.E. (1999). A history of systematic botany in Australia. *In*: Orchard, A.E. (ed.) *Flora of Australia*. Vol. 1 (2<sup>nd</sup> edn.). pp 11–103. (Australian Biological Resources Study: Canberra.)
- Smith, M.G. (2018). Wildlife Conservation (Rare Flora) Notice 2017. Summary of additions, deletions and changes to the notice as of 16 January 2018. Department of Biodiversity, Conservation and Attractions. https://www.dpaw.wa.gov.au/images/documents/plants-animals/threatened-species/Listings/summary\_of\_changes\_to\_rare\_flora\_notice.pdf [accessed 8 February 2018].
- Smith, M.G. & Jones, A. (2018). *Threatened and Priority Flora list 16 January 2018*. Department of Biodiversity, Conservation and Attractions. https://www.dpaw.wa.gov.au/plants-and-animals/threatened-species-and-communities/threatened-plants [accessed 8 February 2018].
- Sprengel, A. (1825). *Opercularia. In*: Sprengel, K. *Caroli Linnaei Systema Vegetabilium*. Vol. 1. (16<sup>th</sup> edn.) p. 385. (Librariae Dietrichianae: Gottingae [Göttingen].)

- Spjut, R.W. (1994). A systematic treatment of fruit types. Memoirs of the New York Botanical Garden 70: 1–182.
- Stafleu, F.A. & Cowan, R.S. (1979). Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types. Vol. 2. (Bohn, Scheltema and Holkema: Utrecht.)
- Rye, B.L. (1987). Rubiaceae. *In*: Marchant, N.G., Wheeler, J.R., Rye, B.L., Bennett, E.M., Lander, N.S. & Macfarlane, T.D. (eds) *Flora of the Perth region*. Part 2. pp. 643–646. (Western Australian Herbarium, Department of Agriculture: [Kensington,] Western Australia.)
- Toelken, H.R. (1986). Rubiaceae. *In*: Jessop, J.P. & Toelken, H.R. (eds) *Flora of South Australia. Part II, Leguminosae-Rubiaceae*. pp. 1059–1076. (South Australian Government Printing Division: Adelaide.)
- Walter, K.S. & Gillett, H.J. (eds) (1998). 1997 IUCN Red List of Threatened Plants. Compiled by the World Conservation Monitoring Centre. (IUCN–The World Conservation Union: Gland, Switzerland and Cambridge, UK.)
- Wheeler, J.R. (2002). Rubiaceae. *In*: Wheeler, J., Marchant N. & Lewington, M. (eds) *Flora of the south west: Bunbury-Augusta-Denmark*. Vol. 2. pp. 864–867. (Australian Biological Resources Study: Canberra.)
- Western Australian Herbarium (1998–). FloraBase—the Western Australian Flora. Department of Biodiversity, Conservation and Attractions. https://florabase.dpaw.wa.gov.au/ [accessed 14 March 2018].
- Western Australian Minister for the Environment (2015). Wildlife Conservation (Rare Flora) Notice 2015. Western Australian Government Gazette 166: 3<sup>rd</sup> November 2015.
- Young, T. (1797). Description of a new species of Opercularia. Transactions of the Linnean Society of London 3: 30-32.